Spawning and development of the Flat-headed Gudgeon *Philypnodon grandiceps* (Krefft, 1864) (Teleostei:Eleotridae).

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ABSTRACT

Flat-headed Gudgeon *Philypnodon grandiceps* were bred in ponds and aquaria at the Narrandera Fisheries Centre at temperatures from 18.0 to 28.0^{0}C. Breeding in inland rivers probably occurs between October and April. An abundant food supply was essential for initiating spawning and the breeding display was recorded.

Eggs were demersal, transparent, telolecithal and an elongated tear-drop shape with an adhesive disc at the pointed end. They measured 1.2 - 2.2 mm in length by 0.7 - 0.9 mm in width, and were attached in clusters to solid objects. Oil globules were small and numerous at first, but coalesced to a single oil globule halfway to hatching. Eggs hatched in 4d 20h to 8d 8h after fertilisation at temperatures of 15.9 to 22.6^{0}C. The total length of larvae at hatching was 3.15 to 4.32 mm and eyes were fully pigmented. The prolarval stage terminated at about 3d 12h after hatching, when length was 3.93 to 4.69 mm. The characteristic dark spot at the base of the caudal fin was present from the mid prolarval stage onwards. Males and females matured at one year old and were short lived. The largest fish collected was 11.0 cm TL. Up to 2020 ova were present in the ovaries and the Gono-somatic Index (G.S.I.) reached a maximum of 11.92 in females.

Key words: *Philypnodon grandiceps*, Flat-headed Gudgeon, breeding biology, spawning, egg and larval development, freshwater fish New South Wales.

Introduction

The Flat-headed Gudgeon *Philypnodon grandiceps* (Krefft, 1864) (Fig. 1a), also known as the Big-headed, Bull-headed or Yarra Gudgeon and Collundera, was at the time of this research, 1968, the only described member of this genus in the family Eleotridae. More recently a second species, the Dwarf Flathead Gudgeon *Philypnodon* sp., has been recognized, but has not yet been formally described (Hoese *et al.* 1980; Pusey et al. 2004). The maximum size of the dwarf species is 5.0cm while *P. grandiceps* grows up to 12cm. Although both belong to the family Eleotridae, some workers place them in the Family Gobiidae, Subfamily Eleotrinae.

In inland New South Wales *P. grandiceps* has been reported in the Lachlan River from Wyangala Dam in the east to Oxley in the west (Table 1) particularly in the water storages associated with this river (Llewellyn 1983). It occurs in the Murrumbidgee River below the Lachlan /Murrumbidgee River junction, and is patchy along the Murray River and into South Australia, but common in the Campaspe River, a southern tributary of the Murray (Humphries and Lake 2000; Humphries *et al.* 2002). It is reported to be patchily distributed in the Darling Basin (Pusey *et al.* 2004). It is frequently recorded in coastal drainages and estuaries in New South Wales, and occurs from the Burdekin system in central Queensland (Merrick and Schmida 1984, Pusey *et al.* 2004), southwards to Adelaide, South Australia, and is also reported from Tasmania (Hoese *et al.* 1980). The Dwarf Flat-headed Gudgeon, *Philypnodon* sp., has a similar coastal distribution to *P. grandiceps*, and in the inland of New South Wales is reported from Bathurst on the Macquarie River and the upper Murrumbidgee River (Pusey et al. 2004).

P. grandiceps is a freshwater species usually confined to lakes, billabongs, lagoons or sluggish weedy margins of rivers. Along the coast it is also found in upper estuarine tidal habitats

P. grandiceps was seldom found in large numbers in the inland and previous observations on their breeding requirements, behaviour or egg and larval development are limited. Preliminary observations have been reported briefly (Llewellyn 1971). The present paper outlines detailed embryonic development of the eggs and larvae of *P. grandiceps* and describes induced breeding and breeding behaviour. These data will assist with identification of immature fish, and give some insight into the environmental requirements for successful breeding. This information is of considerable importance in view of the changes that have taken place in many of our waterways over the last 40 years. Some inland fish larvae are very similar, making identification difficult unless detailed descriptions are available.

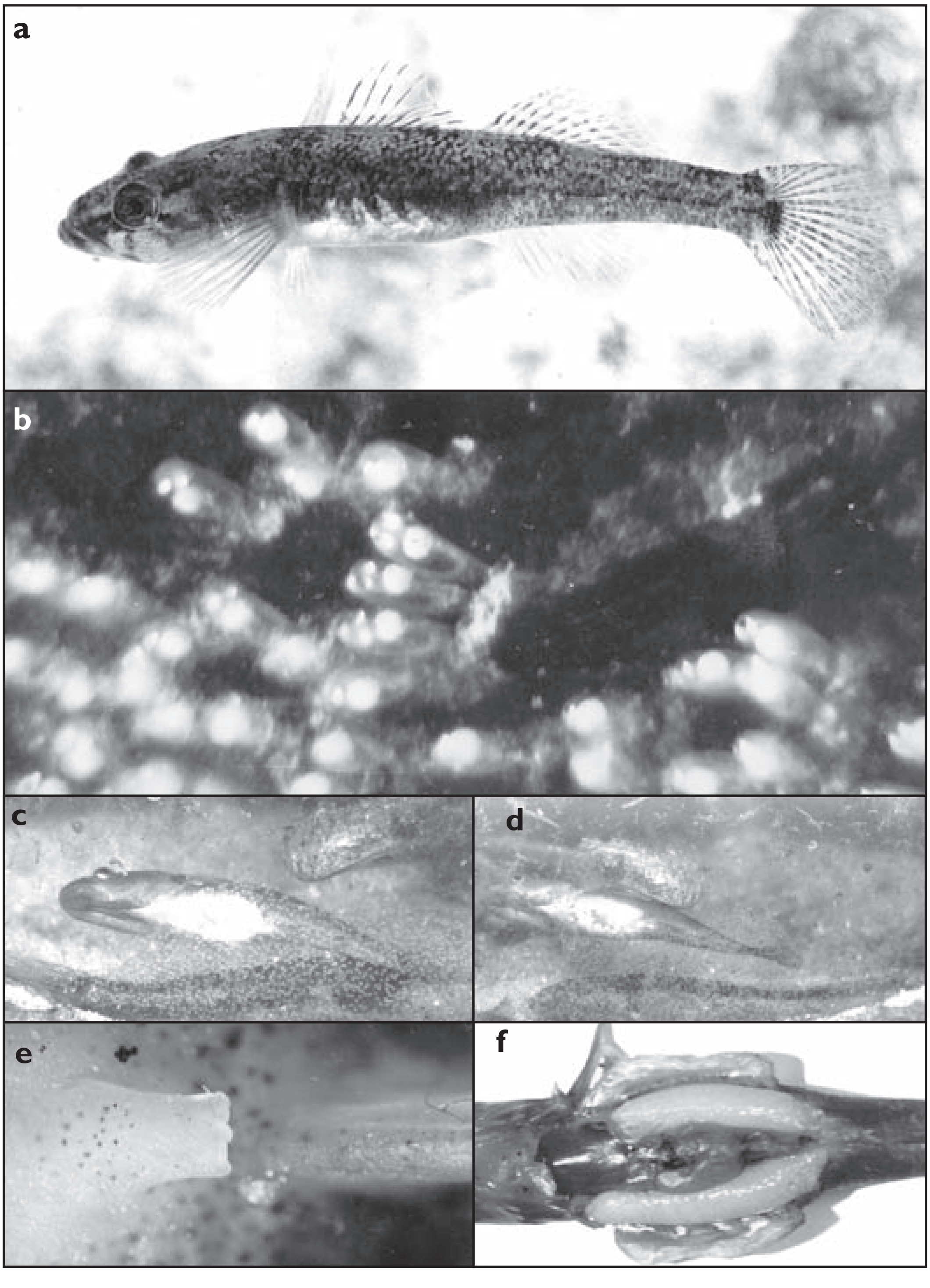

Figure 1. (a) Adult *P. grandiceps*; (b) Close up of cluster of eggs attached to glass of aquarium; (c) Parallel head to tail posture, while female is spawning. Darker male waits below and numerous eggs can be seen attached to glass; (d) Parallel head to tail posture while spawning. Note the almost transparent skin mid ventrally on the abdomen of the female; (e) urinogenital papilla of the male; (f) Dissection showing viscera with ripe testes.

Materials and Methods

Philypnodon grandiceps was caught in the Murray Darling within New South Wales, though numbers were very low, despite extensive sampling using mainly dip nets and haul nets. Only once was it caught in sufficient numbers to commence breeding trials (Table 1). Because of the irregular availability and patchy distribution from the Murray Darling, 52 brood fish were obtained from an eastern watershed, Prospect Reservoir, Sydney to complete the study.

The 4.57 m long haul net and dip net were made of square mesh netting of approximately 0.5cm sides. Fish from the Murray Darling were transported to Narrandera in open 44 gallon drums while fish from Prospect Reservoir were transported in cardboard cartons with polythene liners, using a battery operated aerator pump to supply air.

Since most eleotrids have adhesive eggs which are difficult to collect from the pond environment, only a single pond 0.01ha in area and 137cm in depth was

Table 1. Collection sites for *P. grandiceps.*

Date	Collection Site	No. of Specimens	Comments
*-. -. 59	Wyangala Dam	3	—
*25.ii.60	Lachlan River, Oxley	1	—
*-. -. 62	Wyangala Dam	4	—
19. v. 68	Murray River, Renmark	3	Caught amongst Willow tree roots with dip net
-.viii. 68	Wyangala Dam	3	Collected with a haul net.
#24.xi.68	Lagoon, Euston Common	30	Collected with a haul net
#22.ix.69	Prospect Reservoir outlet	13	Collected with a haul net
#9.x.69	Prospect Reservoir outlet	39	Collected with a haul net
21.iv.70 to 24. vi.72	Lake Cowal	Numerous	—
29. x.72	Lake Brewster	1	—

* Specimens from Narrandera Fisheries Centre collection.
# Used for breeding trials.

stocked. Twelve of the sixteen surviving fish caught within the Murray Darling at Euston were placed in this pond (Table 1). They measured 35.3 to 47.4mm (mean, 39.9mm) in length. The other four, together with 43 surviving out of the 52 Prospect Reservoir fish, were placed in five 90 L aquaria (7,7,8,12,13 in each), which were aerated and contained aquatic plants and some rocks. Fish in aquaria were fed once daily on fresh or frozen earthworms or Mosquito fish *Gambusia holbrooki*, which were sometimes chopped in half. As the breeding season approached it was necessary to increase feeding to twice daily to induce spawning. Although sex could not be determined accurately at this time, approximately twice as many males as females were placed in each aquarium, based on their size and shape. Sampling of the pond to locate eggs and larval stages was carried out at regular intervals to confirm breeding (see Llewellyn 1973, 1974, 1979 and 2005). The pond was lowered on 18.viii.1969, 9 months after the initial stocking of 12 fish, to determine whether breeding had occurred. Wherever possible, measurements of the young and adult fish from ponds were used to determine their approximate growth rate.

Since eggs of this species were thought to be adhesive, greater attention was focused on aquarium breeding. All fish kept in aquaria were watched regularly for signs of any courtship display. The aquaria sides, and rocks within the aquaria, were examined daily for signs of egg deposition. When the fish commenced displaying, constant vigilance was kept until spawning occurred. During the hourly night time inspections a dull red light was turned on during observations to reduce the disturbance caused by fluorescent lights. Natural lighting was maintained for the rest of the time. These aquaria were heated during winter months in an attempt to induce spawning at that time. Using the pond temperatures at the estimated date of the successful pond spawning, aquarium temperatures were fluctuated between 10.0 and 30.0^{0}C. Water temperatures were measured regularly.

Conditions associated with spawning, their behaviour; and egg and larval development were recorded. Eggs, when located, were removed from the substrate using a scalpel, and transferred to Petri dishes in the laboratory at ambient temperatures (see Llewellyn 2005 for details). The time after fertilisation was determined and frequent sketches of the eggs and larvae were made. Where more than three dimensions were taken mean ± Standard Deviation together with number in sample (n) is reported. Some composite photographs were compiled from phase contrast photo-micrographs.

Because of the limited number of fish on hand, only those fish which accidentally died together with a few chosen individuals, could be examined for gonad condition to determine their proximity to breeding. From these fish, lengths, weights, stages of maturation of the gonads, fecundity and Gonosomatic Indices (GSI's) were determined (G.S.I. = weight of gonad X 100/weight of body, Belsare 1962, Mackay 1973).

Results

A complete record of fish collected is shown in Table 1. The only large sample obtained (n=30) from the Murray Darling were caught by haul net in lagoons and billabongs on Euston Common (34^{0}35'E, 142^{0}44'S) 80km west of Balranald on the Murray River floodplain on 24.xi.68. The other brood fish (n=52) were caught by haul net in the outlet to Prospect Reservoir (33^{0}49'E, 15^{0}054'S), 32km west of Sydney in the Georges River system on 22.ix.69 and 9.x.69 (Table 1). Collections from Euston were supplemented with fish from Prospect to provide sufficient fish to attempt to spawn them.

An additional three *P. grandiceps* were collected by dip net on 19.v.68 in the Murray River along the weedy edges amongst the fibrous roots of Weeping Willow (*Salix babylonica*) at Renmark (34^{0} 10'E, 140^{0}45'S), 26km west of the New South Wales / South Australia border (Table 1). A few other individuals which had been lodged in the Narrandera Fisheries Centre (Inland Fisheries Research Station) fish collection between 1959 and 1972 were examined also. These fish had been collected from Lake Cowal, Lake Brewster and Wyangala Dam (Table 1).

Induced Breeding

Pond trials

Following stocking of a pond with 12 Euston fish (length $\bar{x}$ 39.9mm) on 27.xi.68, 38 were recovered from this pond on 18.viii.69, 8½ months later. Since all of this species brought onto the Research Station were accounted for and no other records of this species existed within 200km of the Station, it was concluded that the first and only pond breeding had occurred (Table 2 and Fig. 2). It seemed likely that spawning had occurred around December 1968 when pond temperatures varied from 23.8 - 27.7^{0}C at the surface and 22.5 - 25.2^{0}C at the bottom.

Length measurements from the brood fish taken at the time of stocking and 8½ months later, and the young fish from the time of spawning to capture (8½ months) were used to construct a growth curve (Fig.3). Twenty five of the smaller year class (31-40mm, mean 35.3mm, ±2.30, n=26, Fig. 2)), were returned to a pond for further growth rates and/or breeding but none survived (29.xii.69). Eleven of the 12 remaining adults (51-81 mm, mean 68.6 mm, ±10.62, n=12 Fig. 2) were returned to their pond, one having been taken for gonad examination, but none had survived by 26.vi.70. No further pond observations were made.

Aquarium trials

Initially five aquaria were stocked with 7,7,8,12 and 13 fish respectively. Spawning was only successful in one aquarium which was initially stocked with eight Prospect Reservoir fish. Fourteen separate spawnings occurred in this aquarium between 7.x.69 and 1.v.70. The first two spawnings occurred when six of the eight fish remained alive, but because a further two died, an additional 6 (3 Prospect Reservoir and 3 Euston fish from other aquaria) were added to this aquarium making a total of ten. Breeding re-commenced, when the numbers dropped to eight, and continued spasmodically until May. In all aquaria, fish frequently died.

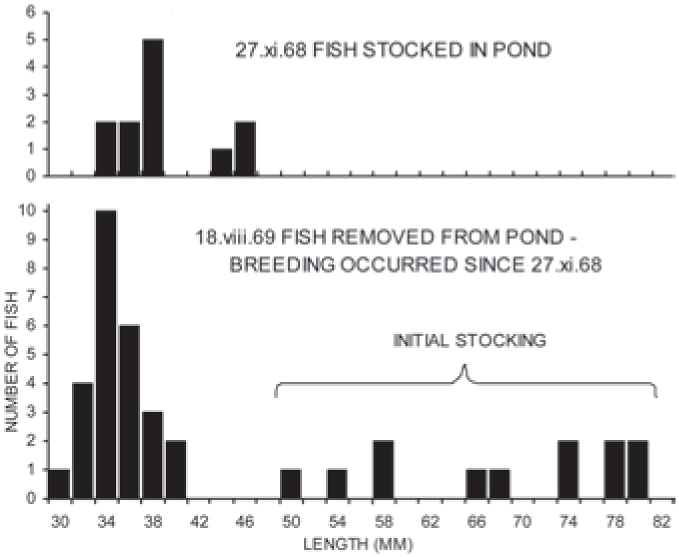

Figure 2. Length/frequency of total population of fish stocked in a pond on 27.xi.68 at the Narrandera Fisheries Centre and later removed from the same pond on 18.viii.69 after a successful breeding.

Fish spawned in the aquarium between temperatures of 18.0^{0} and 28.0^{0}C (see Table 2) after two weeks of intensive feeding. Without intensive feeding spawning did not occur. The temperature regime in heated aquaria during April and May 1970, when 3 successive spawnings occurred is shown in Fig. 4. On all occasions spawning occurred during periods of rising water temperature (Fig. 4). Fish showed no diurnal preference when initiating spawning. Likewise photoperiod seemed to have little effect as they readily spawned in mid-winter when heated aquaria were used.

Table 2. Successful breeding of *P. grandiceps* (app. = approximate date. Time found (h) = time of day eggs first sighted).

Date	Time found (h)	Location	Temperature ^{0}C	Comment
-.xii.68app.	—	Pond	—	12 adults stocked on 27.xi.68, 40 retrieved from pond on 18.viii.69. Euston fish.
7.x.69	2150	Aquarium	19.5	Egg development well advanced when found; approx. 600 eggs spawned, Prospect fish
11.xi.69	1345	Aquarium	21.0	Just spawned, Prospect fish
*28.xi.69	1455	Aquarium	19.5	—
22.xii.69	0845	Aquarium	24.5	Well developed eggs
1.i.70	0210	Aquarium	22.2	Just spawned, 800 eggs
10.i.70	1200	Aquarium	25.1	Eight cell stage
19.i.70	1800	Aquarium	26.0	Well developed eggs
3.ii.70	0800	Aquarium	28.0	Cap stage
2.iii.70	afternoon	Aquarium	26.8	Eggs well developed when found.
9.iii.70	0900	Aquarium	22.1	Early embryo in eggs when found.
18.iii.70	0645	Aquarium	23.2	Cap stage
12.iv.70	0800	Aquarium	19.7	Spawning started at 0130h
27.iv.70	1320	Aquarium	18.0	Just spawned
1.v.70	2100	Aquarium	22.9	Cap stage, 350 eggs spawned

* All breeding after 28 xi 69 had a mixture of Prospect and Euston fish in the same tank.

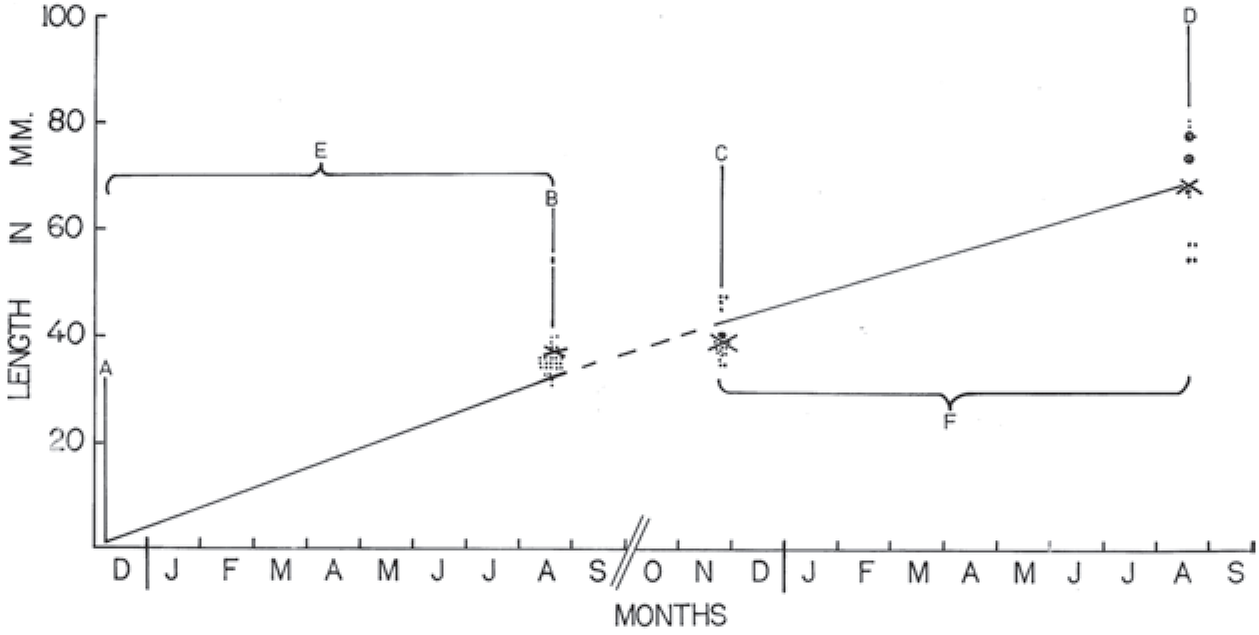

Figure 3. Growth in length of *P. grandiceps* determined from adult fish stocked in a pond and the young they produced. A - approximate month of spawning based on water temperatures (i.e. above 18°C after 10.x.68); B - length of juveniles in month they were retrieved from pond; C - month the adults were stocked in ponds; D - adults the month they were retrieved from pond; E – length of time young fish were free 27.xi.68 -18.viii.69; F – Length of time adults were free 27.xi.68 -18.viii.69; X – mean lengths.

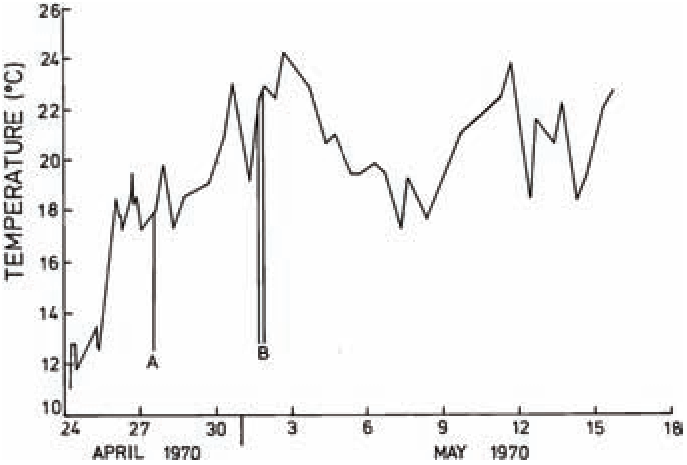

Figure 4. Daytime aquarium temperatures during April and May when two successful breedings occurred. The aquarium was artificially heated. A, first breeding; B, second breeding in which two spawning attempts were made by the same fish.

Breeding displays

Pre-spawning displays were first observed on 9.xi.69, and were closely followed between 23 and 28.iv.70, during which period temperature rose from 11.7 to 19.7°C (Spawning A. Fig. 4).

Breeding displays were only observed at temperatures above 17.5°C after a continuous period of intensive feeding. Detailed observations commenced on 23.iv.70 at 0900 hours at a water temperature of 19.5°C and lasted four days. Two fish were observed lying horizontally side by side facing in the same direction in a hollow nest in the sand along the vertical side of the aquarium (Fig. 1d). A side to side head to tail posture was also frequently adopted either in a vertical or horizontal attitude (Fig. 1c). The largest of the pair, which turned out to be the male, was 90mm long and became almost black in colour with its darker markings still visible (Fig. 1c & d).

Fish maintained their nest site even when a sudden drop of temperature to 11.0°C occurred. The water temperatures then rose steadily from 25 April (Fig. 4), and fish were examined hourly. The fish remained in the sandy depression regularly alternating the head to head and head to tail positions for the next 3 days. The male moved about the aquarium more frequently than the female particularly during darkness but regularly returned to the nest. The female remained in the nest, except when feeding early in the morning. On the few instances, where both fish left the sandy depression simultaneously, one would guard the area from a distance. The male frequently chased away intruders returning to the nest promptly, and their territory increased in size as time progressed. On 27th April at 18.5°C (Fig. 4) at 0730h the female made her first wriggling motion beneath the male. The papilla of the female was now half the length of the anal fin, and hung downwards pointing posteriorly at an angle of 60 degrees. The female became quite active and turned on her side at regular intervals so that her abdomen faced the glass for a few seconds at a time while squirming, fanning and cleaning the glass with her pectoral fins, and became very agitated when the male left the nest (dimensions 22x12x7cm). Within 2h of the first wriggling motions the female underwent spasmodic "yawning bouts", when she expelled clouds of white flaky material from the mouth. The male and female frequently faced each other near the nest angled at 90° to 120°, pointing upwards with their fins extended. They rolled over on their sides the female swimming alongside the male, facing him ventrally. Following a rapid tail flick they spiraled around the longitudinal axis between each other, increasing in speed until after one revolution, they darted off in opposite directions. The female also often wriggled when beside the male and then swam around in unison in a tight circle ceasing when the wriggling became quite intense. Spawning commenced at 1320 and continued to 1700h. The rate of ova deposition and the frequency of spawning runs, in which the female remained with her abdomen towards the spawning surface while waiving her urinogenital papilla across it (Fig. 1c and d), peaked at 1400h and became spasmodic towards the end. One hundred and twenty one ova were laid during 11 spawning runs taking up a total time of 6m 23s (see Fig. 1b). The longest spawning run was 1m 20s when 20 ova were deposited and the shortest was 11s when 4 ova were deposited. The mean rate of ova deposition during these runs was 1 ovum per 3.2 seconds (1 ovum per 1.4 to 20 sec). Between 1328h and 1417h spawning runs were longest, the duration of spawning runs of females and fertilisation periods of males were as follows:- (F) 7m, (M) 13s; (F) 7m, (M) 8s; (F) 4m 20s, (M) 15s; (F) 18s, (M) 9s. The ratio of time spent spawning to time spent fertilising was approximately 22:1. At times the female appeared to push the male towards the eggs in an attempt to encourage the male to fertilise them. During both the pre spawning and spawning period the male was very aggressive towards intruders and chased them away from the nest and often around the aquarium. The female remained at the nest during the entire spawning period.

At 1530h the male became antagonistic towards the female in the nest area, although the female continued to occasionally deposit ova up until 1700h. She left the nest for the first time at 1708h to chase off an intruder and on returning, the male met her in mid water and in a parallel head to tail posture, carried out a rapid spiral around the longitudinal axis between each other. The male immediately returned to the nest (1710 h) and from then on repeatedly chased the female away when she attempted to approach the nest. The male fanned the eggs with the pectoral fins and guarded them until hatching was complete, when temperatures were between 17.2 and 23.0⁰C. Hatching occurred during the 3rd to5th day after spawning (30.iv.70 to 2.v.70).

A second spawning between a different pair occurred in the same aquarium on 1.v.70 (Table 2) when the water temperature was 22.9⁰C, resulting in three hundred and fifty ova of which all but eight hatched within 3.5 to 8 days (Fig. 4(B)). Spawning was similar to that already described, but the small female still remained aggressive to other fish and displayed the yawning posture, even after the male had chased her from the nest on completion of spawning. This female died 3 days after spawning.

In a third spawning 600 ova were laid over an area of $39cm^2$. In a fourth spawning, which was a failure, the temperature was 19.5⁰C, and the male wouldn't fertilise the ova, the female didn't attach many ova to the substratum and many ova were eaten by the male.

Embryonic development of eggs

At least some of the eggs described here are from Euston fish, however the parental origin of the remainder (Prospect Reservoir or Euston) is uncertain. Timing and stages of embryological development are outlined in text and figures as a guide for aging and for identification purposes. The eggs of *P. grandiceps* (Fig. 5) were transparent, elongated tear-drop shaped, demersal and possessed a disc at the truncated narrow end comprised of adhesive strands (Fig. 6b), which soon became matted into a thick mass (Fig. 6c). The remainder of the chorion was non-adhesive with a pitted surface under phase contrast microscopy (Fig. 7c). Shortly after spawning, during bipolar differentiation,

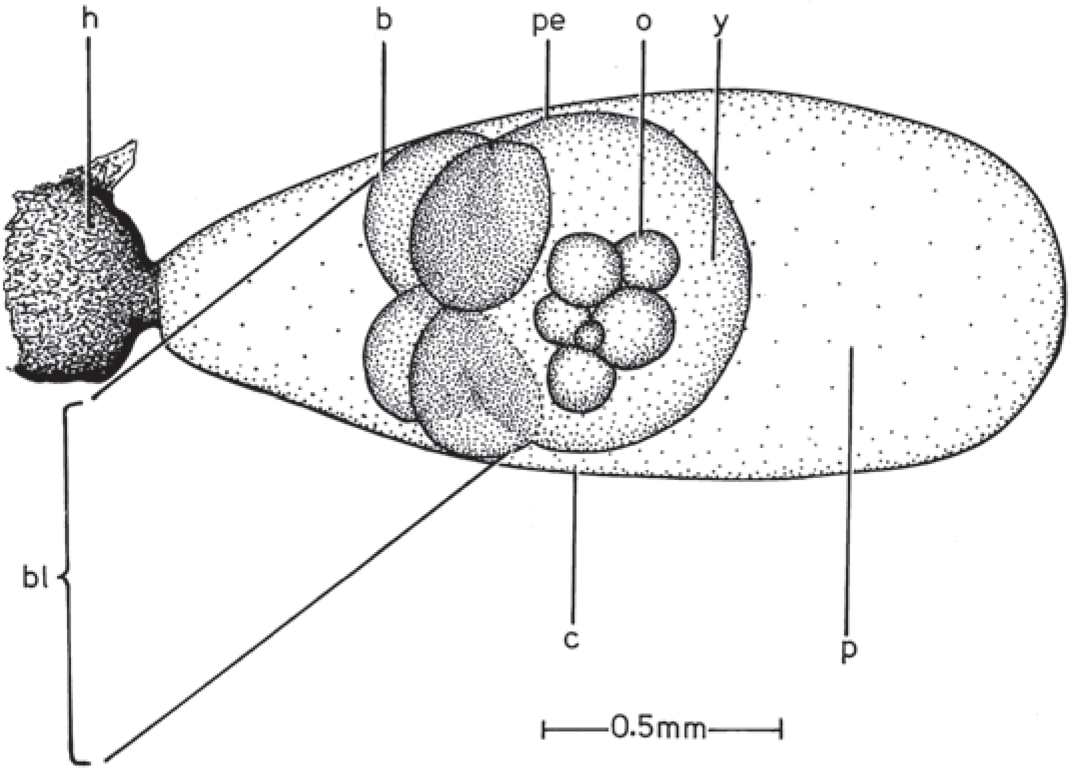

Figure 5. Egg *of P. grandiceps* 2h 17m after fertilisation (four cell stage). b, blastomere; bl, blastodisc; c, chorion; h, adhesive disc; o, oil globule; p, perivitteline space; pe, extraembryonic periblast; y, yolk.

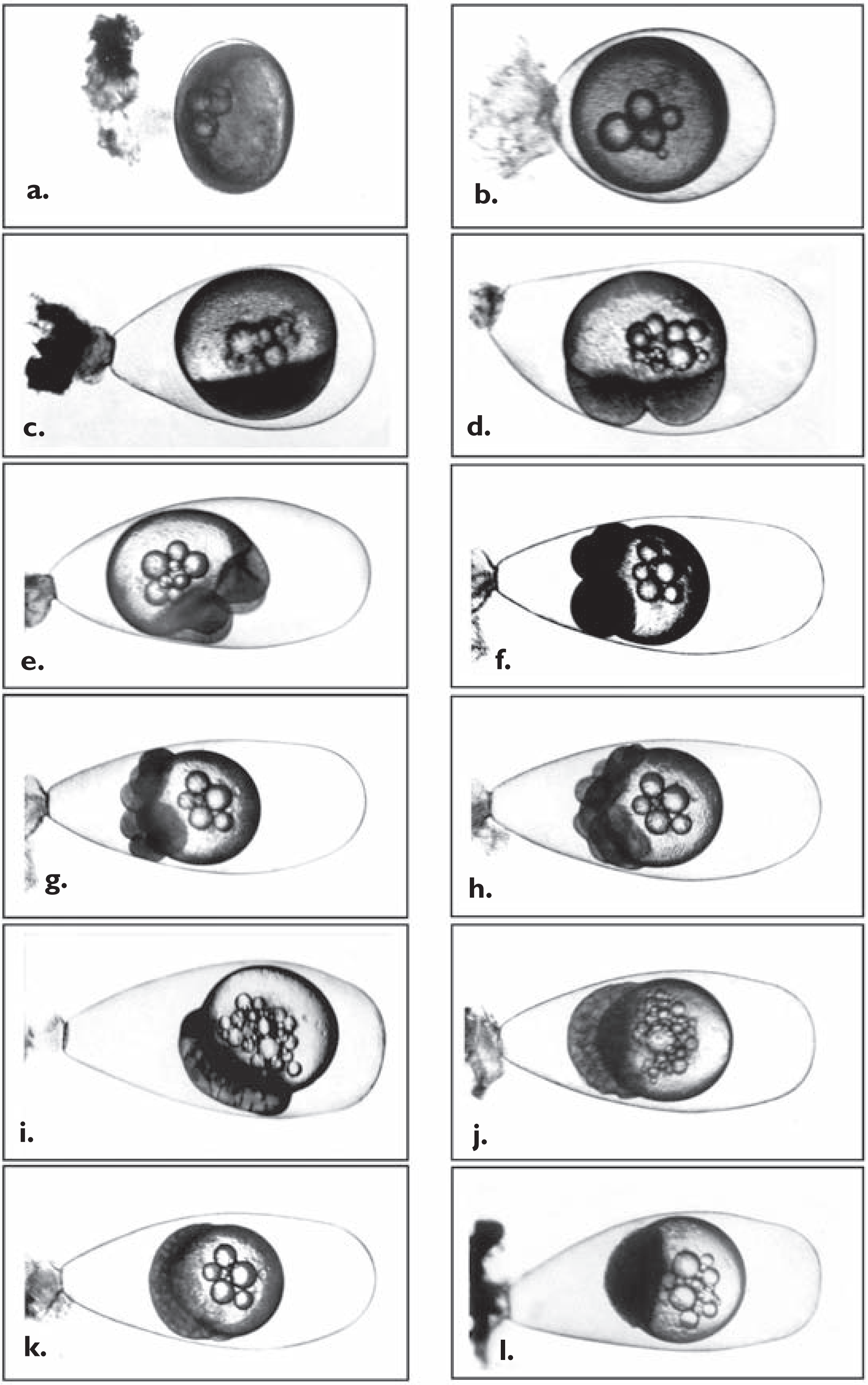

Figure. 6. Eggs of *P. grandiceps*, times given are after fertilisation (d = days, h = hours and m = minutes). (a) 0m - before chorion starts to enlarge; (b) 1h 5m - chorion nearly fully enlarged; (c) 1h 35m - 1 cell stage; (d) 1h 56m - 2 cell stage: (e) 2h 9m - cells dividing into 4 cell stage; (f) 2h 17m - 4 cell stage; (g) 2h 28m - 8 cell stage; (h) 2h 44m - 16 cell stage; (i) 3h - approximately 32 cell stage; (j) 3h 15m - approximately 64 cell stage; (k) 4h 5m - individual cells still visible but too numerous to count; (l) 9h 53m - early blastoderm with individual cells no longer visible.

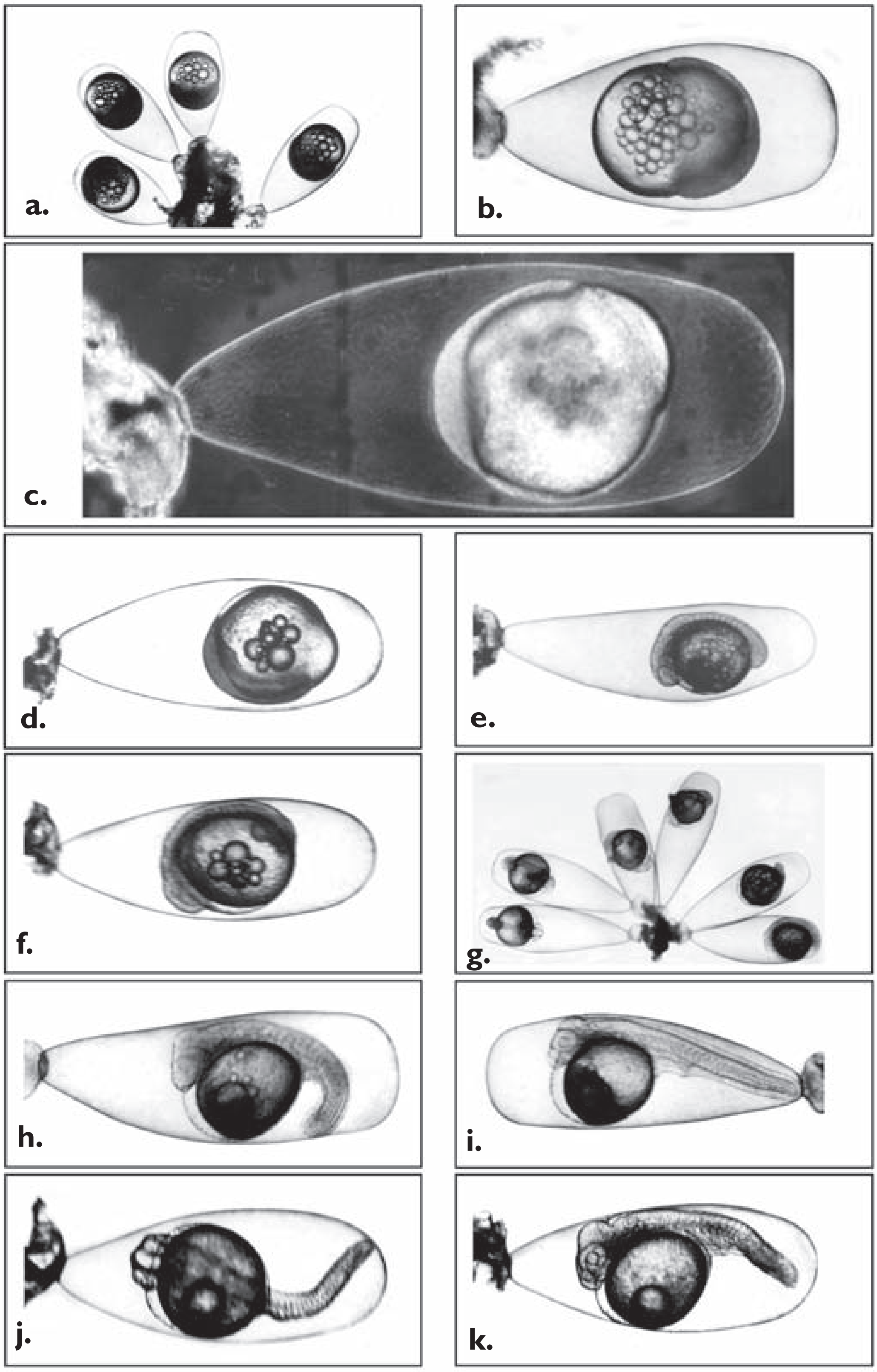

Figure 7. Eggs of *P. grandiceps*, times given are after fertilisation (d = days, h = hours and m = minutes). (a) 17h 30m - cluster of eggs showing commencement of epiboly; (b) 18h - epiboly with blastoderm half covering the yolk; (c) 23h 25m - phase contrast of early formation of yolk plug and blastoderm thickening, indicating the commencement of neurulation; (d) 23h 45m - yolk plug and early embryo; (e) 1d 24m - enlargement of cephalic region of early embryo, and appearance of optic lobes and somitic divisions of tail; (f) 1d 4h - enlargement or abnormality in the tail region; (g) 1d 6h - cluster of eggs showing well defined optic vesicles and larvae $^{2}/_{3}$ of the way around the yolk; (h) 1d 9h - subcaudal fold and commencement of coalescence of oil globules; (i) 1d 19h - coalescence of oil globules nearly complete, eye lens, anus, and fin folds visible; (j) 1d 20h 30m - coalescence of oil globule complete; (k) 1d 20h 30m - otic capsule first visible and pericardial sinus large.

little re-organisation and redistribution of oil globules occurred. The egg was heavily telolecithal giving rise to meroblastic or discoidal cleavage.

Most newly spawned ova were nearly spherical possessing no perivitteline space (Fig. 6a). On contact with water and after fertilisation, distension and then hardening of the chorion occurred. This process gave rise to the large perivitteline space at the proximal and distal ends of the egg (Fig. 6 b and c). The eggs distend along the axis passing through the basal disc (Fig. 8 plot B; cf. plot A).

Several abnormalities in development occurred at water temperature of 15.9 to 22.6^{0}C. Rate of development was greater at higher temperatures (see also Piavis 1961, Lagler et al. 1967, Edsal 1970), and higher egg mortalities occurred below 17.0^{0}C and above 23.0^{0}C.

Newly spawned ova, which were equivalent to the yolk dimensions, were sometime slightly flattened (Fig. 6a) (diameter $\bar{x}$ 0.72 ±0.08 x $\bar{x}$ 0.83 ±0.09mm (n=20), range 0.51 - 0.85mm x 0.70 – 1.04mm). When water hardening and distention was complete their size increased substantially ($\bar{x}$ 1.79 ±0.30 x $\bar{x}$ 0.73 ±0.04mm (n=38), range 1.15 - 2.17mm in length and 0.69 - 0.90mm in width) (Fig. 8). The width of the egg was only slightly larger than the diameter of the yolk. After water hardening the external dimensions do not change, except when the egg becomes flaccid and misshapen just prior to hatching.

The oil globules varied in number from 5-40 (diameter $\bar{x}$ 0.16 ±0.05mm, n=16, range 0.07-0.24mm) and were situated centrally in the yolk throughout the early stages of development. The yolk was normally situated centrally within the chorion but occasionally it became lodged at the distal end of the egg (Fig. 7a). The thickness of the chorion was 0.007mm

The blastomeres usually started to form on the flatter area of the yolk (Fig. 6c, d and e). The first cell (0.67 x 0.22mm) occurred at 1h 35m (Fig. 6c) but at low temperatures (15.0^{0}C), it took 2h 40m. The first three cleavages forming the two (cell diameters 0.34 x 0.22mm Fig. 6d), four (0.31 x 0.22mm Fig. 6 e,f) and eight (0.24 x 0.22mm Fig. 6g) cell stages occurred at 1h 43m, 2h 9m and 2h 26m respectively at 20^{0}C. Cleavage periodicity could not be followed easily after this time although the general pattern of development could.

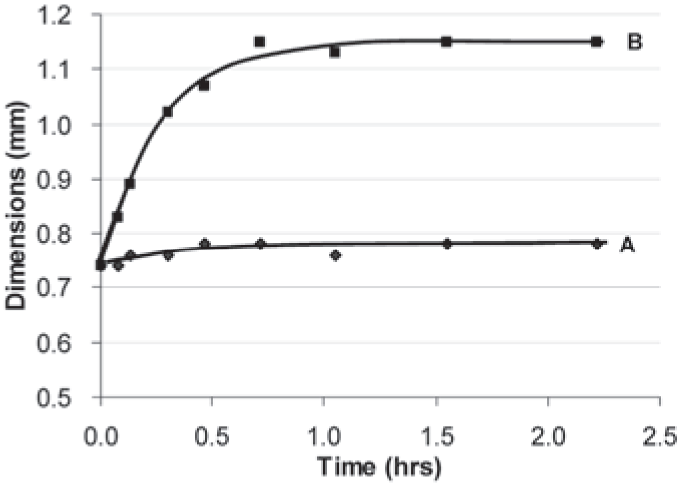

Figure 8. Distension or swelling of chorion of single egg during water hardening immediately after spawning plotted against time. A◆———◆ width of egg which shows little or no change; B■———■ length of egg.

The blastoderm (knob of cells) (Fig. 6h and i estimated as 16 and 32 cell stage), continued to multiply (Fig, 6j and k) until the individual cells were no longer visible (Fig. 6l) (knob of cells 0.62 x 0.34mm). The blastoderm then started to flatten out forming a cap as it spread over the yolk (Fig. 7a) marking the onset of epiboly. This cap half covered the yolk at 18h after fertilisation (Fig. 7b). The thickening of the germ ring forming the embryonic shield commenced when the blastoderm covered ⅔ of the yolk (Figure 7c and d) at around 23h 35m. The formation of a yolk plug was now apparent, marking the approach of blastopore closure. This stage was accompanied by thickening of the neural tube area and the commencement of neurulation. Blastopore closure occurred at the completion of epiboly at approximately 1d after fertilisation. Little tissue differentiation had occurred up to this stage (embryo 0.72 x 0.17mm).

Differentiation of tissues into organs (organogenesis) commenced at 1d 24m (Fig. 7e) and followed a similar general course to that described for other teleosts (e.g. Kuntz and Radcliffe 1915-16; Lagler 1956; Manner 1964), though the timing of appearance of organs, and their size and shape vary between species and are therefore described below for this species. When the embryo was half way around the yolk (embryo 1.08 x 0.07mm), the enlarged cephalic region, the optic vesicles and the division of the caudal region into myomeres became clearly visible (Fig. 7f and g). The subcephalic and subcaudal folds were well formed (Fig. 7h) at 1d 9h. At this point the oil globules commenced to coalesce (Fig. 7i, j, and k) usually leaving only a single oil globule 11h later (0.25mm in diameter). At 1d 19h the eye lenses in the optic vesicles, the dorsal and ventral fin folds, and the anus were clearly visible (Fig. 7i) when the embryo was approximately ¾ the length of the egg (embryo 1.50mm long). The pericardial sinus and the otic capsules were now discernible (Fig. 7k). A vitteline blood vessel appeared (Fig. 9a) and the first movements of the tail and a beating heart were noticed (Fig. 9b) at 2d 4h 44m, when the embryo had reached approximately the length of the egg. The embryo was 1¼ times the length of the egg when the otic capsules were clearly visible (Fig. 9c). Shortly after at 2d 18h 50m the fin folds increased in area and the eyes darkened (Fig. 9d). Resorption of the yolk now speeded up (see irregular resorption Fig, 9e). When the embryo was 1½ times the length of the egg (3d 4h), the beating heart was clearly visible (Fig. 9f) (rate varied between 110-234 bpm (beats per minute) between 3d and hatching). At 3d 13h fin buds first appeared (Fig. 9g and h). The lower end of the intestine situated posterior to the yolk was well developed and the pericardial cavity was increasing in size (Fig. 9i). At 4d the eyes were completely pigmented and the body was 1⅔ the length of the egg (Fig. 9j). The larvae were now

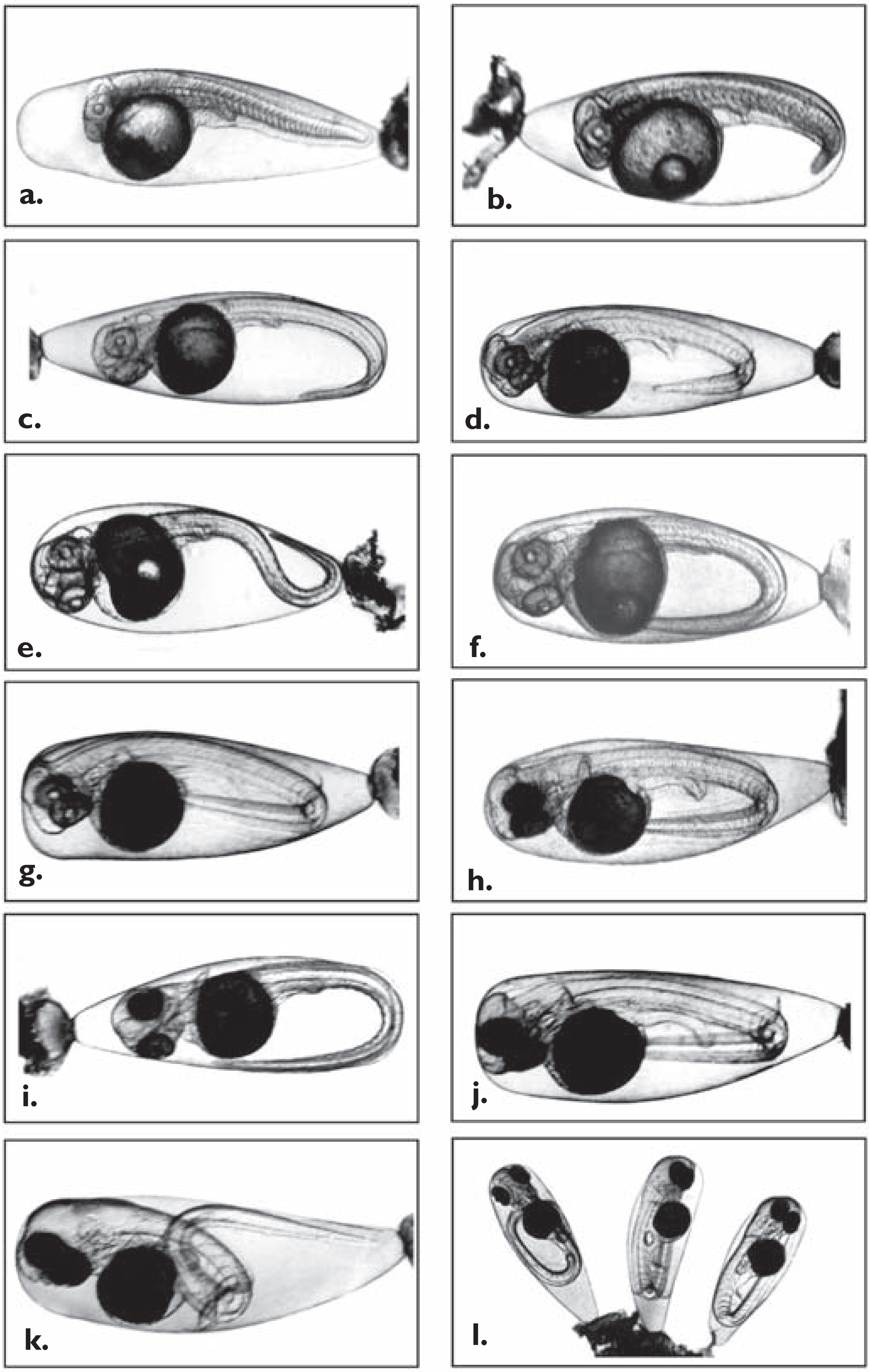

Figure 9. Eggs of *P. grandiceps*, times given are after fertilisation (d = days, h= hours and m=minutes) (a) 1d 23h 24m - vitelline blood vessel; (b) 2d 4h 44m - movement of tail commenced, and pronounced head region apparent; (c) 2d 13h 30m - otic capsule distinct and length of larvae more than length of egg; (d) 2d 18h 50m - fin fold increasing in area and eyes starting to darken; (e) 2d 20h 25m - showing resorption of yolk from the pericardial region; (f) 3d 4h - heart clearly visible and the body 1½ times the length of the egg; (g) 3d 13h 5m - fin buds first apparent; (h) 3d 15h - fin buds clearly visible as are the somitic divisions of the vertebral region; (i) 4d 10m - noticeable bulge in the pericardial region; (j) 4d 10m - large fin fold and eyes now fully pigmented; (k) 4d 6h 10m - first appearance of swim bladder and larva quite active; (l) 4d 13h 48m - group of three eggs showing swim bladder clearly visible and body of larva nearly twice the length of egg.

active and could turn within the egg. The swimbladder and otoliths within the otic capsules were now visible (Fig. 9k). Dimensions for egg structures at 4d 4h are below[1]. At 4d 14h three melanophores appeared dorsally on the swim bladder, blood corpuscles were seen moving within the major blood vessels and a small vesicle yellow in colour (the liver) appeared just posterior to the yolk (Fig. 9l right egg). At 4d 20h, the first hatching occurred in Petri dishes (Fig. 10a and b). However some parent reared eggs hatched at 3½d possibly expedited by physical agitation by the parent. At hatching, the larvae spasmodically but rigorously flexed the tail and wriggled while the fins beat almost continuously. This distorted the chorion (Fig. 10e) and finally fractured it distally (Fig. 10a and b and 11a). The prolarva was free within 10s of this occurring and often took a short time to straighten its body. Occasionally the chorion fractured proximally, remaining around the head end of the prolarva and prolonging shedding time (Fig. 11 b and c). Large numbers of ciliates often clustered around older live eggs as hatching approached (Fig. 10e).

Occasionally, at low temperatures, hatching time was extended a further 3½ days. This not only gave rise to slower development, but also more advanced development taking place in the egg which resulted in a shorter prolarval stage. In these cases egg development continued as follows. At 4d 21h the gill chamber elements appeared and the pectoral fins were well developed (Fig. 10c and d). From 5d onwards after reshaping and streamlining of the yolk sac had occurred, it diminished rapidly (Fig. 12). At 5d 17h a melanistic network appeared dorsally over the swim bladder, and melanophores appeared along the ventral edge of the notochord (Fig. 10 f and g). By 6d 9h the melanophores along the notochord often formed a continuous line and the otic capsules protruded markedly (Fig, 10 g). Within 10h the melanistic net over the swim bladder had fused to form a black dorsal covering (Fig. 10 h). In some larvae during this period the oil globule broke up into smaller globules and dispersed, and the elements of the jaw appeared (Fig. 10i). At 7d 9h the embryo was more than twice the length of the egg (Fig. 10 j). The gill arches could now be seen and more pigment was laid down near and just posterior to the pericardial sinus (Fig. 10k). The oldest egg recorded was 8d 9h after fertilisation (Fig. 10 l) which had been kept at a low temperature (17.4^{0}C).

The heart rate at hatching varied between 150 and 234 b.p.m $\bar{x}$187 ±31.00, n=8) at 19.4^{0}C.

Prolarva

Hubbs (1943) described the prolarva (Fig. 13) as the larva after hatching, up until the time all the yolk was utilised. Eggs that hatch at a very late stage of development probably due to low temperatures and lack of agitation (Fig. 10 k and l) result in a shortened prolarval stage and a large larval length at hatching. At hatching, prolarvae varied from 3.15 to 4.32mm in length $\bar{x}$ 3.71 ±0.44, n=11 and at the end of the prolarval stage were between 3.93 and 4.69mm, $\bar{x}$ 4.19mm ±0.34, n=5 (Fig. 15 A). The growth of larvae from hatching to death was described by the linear regression $y= 0.007x +3.778$ ($r^2=0.326$, $p=0.004$) Figure 15, where y is the length of larvae in mm and x is the hours after hatching. Yolk utilisation sped up just before hatching and changed the shape of the yolk so that the larva became more streamlined: the length of yolk exceeding the depth (Fig, 12). The yolk was completely used up between 2d 12h and 4d 14h after hatching (see Fig. 12D approx. 100h), when active feeding commenced, which indicated the termination of the prolarval stage and the commencement of the post larval stage.

Recently hatched larvae had a specific gravity close to that of water. They swam upwards at a 45^0 angle in bursts of about 10s and then rested for a couple of seconds sinking very slowly in a horizontal attitude, and then repeating this until they reached the water surface. Then they slowly sank to the bottom gradually attaining a head down attitude. During descent they soon learned to swim forward in a horizontal attitude for 5 to 20cm and then continue their descent. Within 1d of hatching they continually swam around and became very active, though some strong larvae behaved in this way immediately after hatching. At 3d 8h after hatching most larvae congregated in the bottom 2.5 cm of the water column during darkness.

The survival of three batches of eggs, observed from the time of fertilisation to just after hatching (Fig. 14 A, B and C), indicated that heaviest mortalities occurred just prior to hatching and during the hatching period (Fig, 14 D to E), with only 21.5% of larvae remaining alive after hatching was complete. The other critical time for larvae was during the change from endogenous to exogenous feeding at the end of the prolarval stage. All the remaining larvae in aquaria died shortly after this stage of development.

The general structure of a P. grandiceps prolarva is depicted in Fig. 13. During prolarval development, water temperatures varied between 19.0 and 26.2^{0}C. At low temperatures growth rate and utilisation of yolk decreased (Fig. 16g, 17g and 18a large amounts of yolk remaining). At hatching the eyes were heavily pigmented and the yolk sac was large (Fig. 11b, c, d and e). Also the fin fold was fully formed (Fig. 11e), the pectoral fins were present and functional (Fig. 11d), the elements of the jaw and mouth were discernible (Fig. 11d and f) and the pumping heart was clearly visible (Fig. 11e and h). The numbers of melanophores which lay along the dorsal and ventral edges of the notochord and tail musculature were variable, and the myotomal divisions were not always clearly visible (Fig. 11f and g). Curvature of the tail region (kyphosis) was common at hatching and occasionally persisted for a short time (Fig. 11g). The dimensions of structures at hatching are provided below[2]. The otoliths

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[1] At 4d 4h the mean dimensions in millimetres of the organs of ten larvae within the egg except where indicated otherwise were as follows:- yolk, width $\bar{x}$0.43 ±0.02, length $\bar{x}$0.44 ±0.04; head width $\bar{x}$0.49 ±0.03; larva length 3.25 n=1; eye $\bar{x}$0.26 ±0.02 x 0.20 ±0.02 n=7; lens diameter $\bar{x}$0.08 ±0.02, n=7; oil globules smallest $\bar{x}$0.04 ±0.001 n=9, largest $\bar{x}$0.18 ±0.01 n=9; swim bladder length $\bar{x}$0.15 ±0.02, depth $\bar{x}$0.10 ±0.01 n=3; and base of ova to which adhesive strands were attached $\bar{x}$0.14 ±0.03.

[2] At hatching the dimensions in millimetres of various structures of the prolarvae were as follows:- yolk depth 0.30 - 0.52 $\bar{x}$0.39 ±0.10, n=4), yolk length 0.42 - 0.56 $\bar{x}$0.47 ±0.05, n=5; oil globule 0.20; swim bladder length 0.18; otic capsule 0.14; eye diameter 0.25; liver 0.07; head depth 0.47; and caudal fin depth including fin fold 0.33.

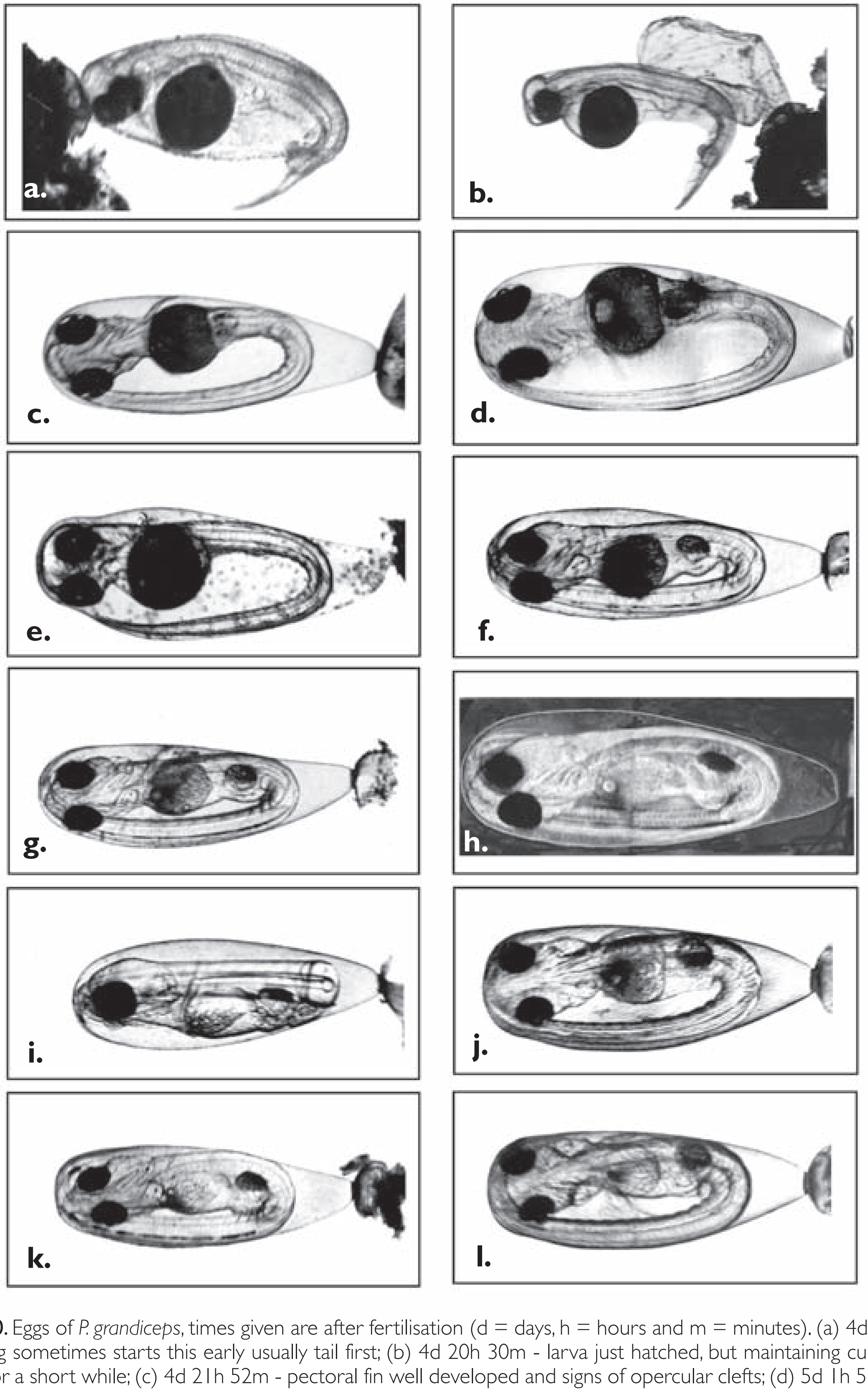

Figure 10. Eggs of *P. grandiceps*, times given are after fertilisation (d = days, h = hours and m = minutes). (a) 4d 20h 30m - hatching sometimes starts this early usually tail first; (b) 4d 20h 30m - larva just hatched, but maintaining curvature in the tail for a short while; (c) 4d 21h 52m - pectoral fin well developed and signs of opercular clefts; (d) 5d 1h 5m - phase contrast, gill arches and eye lenses now visible; (e) 5d 5h 24m- ciliates attacking egg shell frequently occurs as hatching approaches; (f) 5d 17h 25m - otoliths visible in otic capsules and melanophores appear ventral to the notochord; (g) 6d 9h - melanistic network on dorsal surface of swim bladder and otic capsule large and protruding; (h) 6d 20h 40 m - phase contrast showing fusion of the melanistic net over swim bladder and reduction in size of yolk; (i) 7d 2h - breaking up of oil globule as yolk disappears and jaw elements clearly visible; (j) 7d 9h - dorsal view of larva showing shape of diminishing yolk; (k) 7d 12h 30m - considerable reduction in quantity of yolk and gill arches clearly visible; (l) 8d 8h - dorsal view of larva showing considerable loss of yolk and larva coiled approximately 2¼ times within egg.

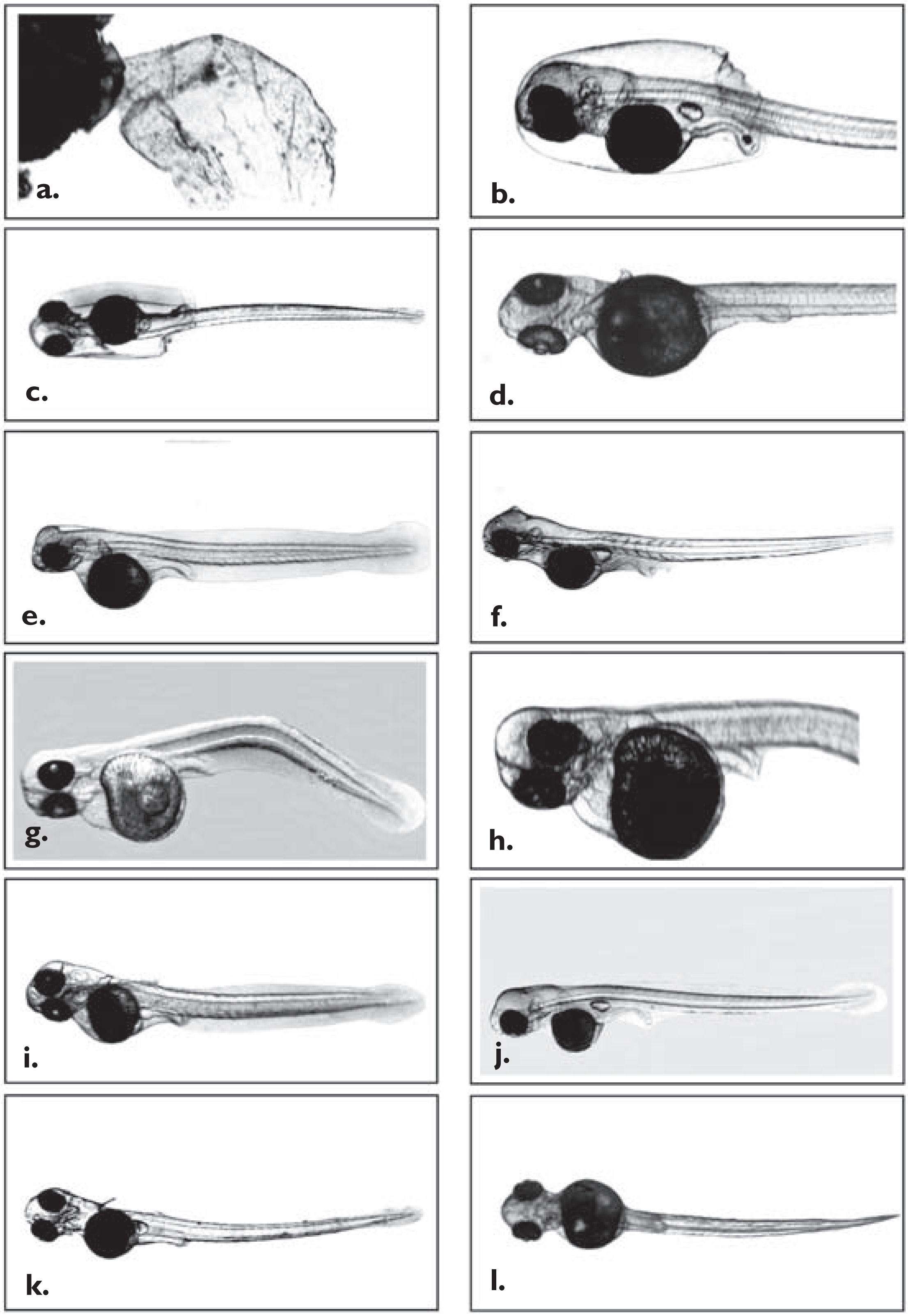

Figure 11. Larvae of *P. grandiceps*, times given are after hatching (d = days, h = hours and m = minutes). All larvae described are from eggs hatched at approximately 6d after fertilisation. (a) 0m - collapsed chorion still attached to substratum; (b) 0m - prolarva just hatched with chorion still surrounding anterior end; (c) 0m - prolarva with chorion still surrounding head and with caudal fin fold well developed; (d) 0m - the structure of the eye, heart and pectoral fin clearly visible; (e) 0m - the shape of the brain and the extent of the fin fold clearly visible; (f) 15m - mouth and jaw elements, the small vesicle below the swim bladder and the dorsal and ventral rows of pigment along the tail well formed; (g) 1h 5m - kyphotic condition persisting well after hatching; (h) 2h 30m - large pericardial sinus and heart present; (i) 2h 30m - divisions of myotomes and the otoliths within the otic capsules visible; (j) 6h 15m - brain of larvae showing prosencephalon, mesencephalon and metencephalon; (k) 8h 10m - gill cleft and branchiostegal rays; (l) 10h 55m - ventral view of larva showing protuberant eyes.

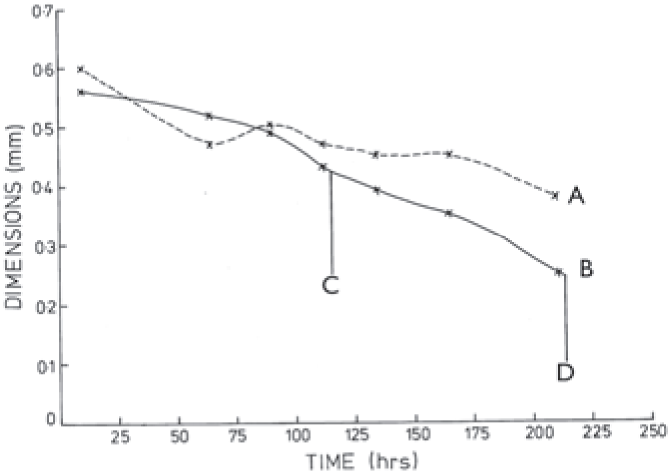

Figure 12. Relationship between length of yolk sac(------------ A.) and depth of yolk sac (————— B.) and hours after fertilisation for a single egg. C, time at hatching; D, time at commencement of exogenous feeding (i.e. yolk completely absorbed).

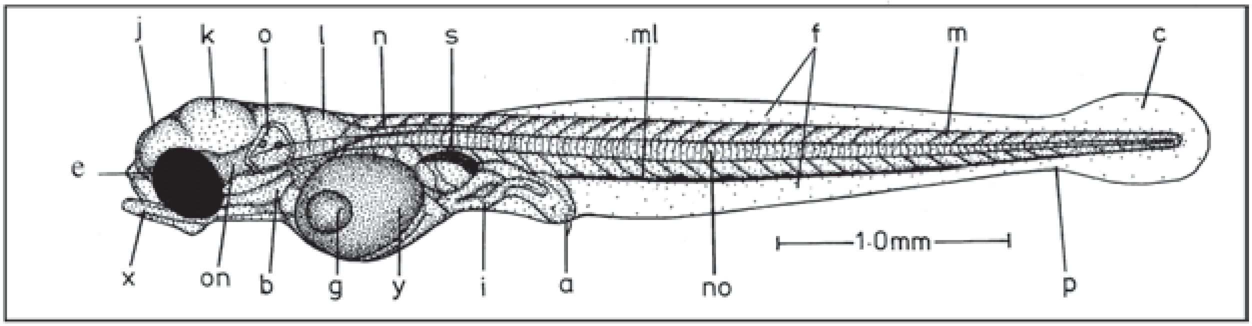

Figure 13. Prolarva of *P. grandiceps* 23h 24m after hatching. a, anus; b, buccal cavity; c, caudal fin fold; e, eye; f, fin fold; g, oil globule; i, intestine; j, fore-brain; k, mid-brain; l, hind-brain; m, myotomes; ml, line of melanophores along ventral edge of musculature; n, neurochord; no, notochord; o, otic capsule possessing otoliths with pectoral fin superimposed over it; on, optic nerve; p, wasting of fin fold to form caudal peduncle; s, swim bladder with melanistic dorsal wall; x, lower jaw; y, yolk.

within the otic capsules (Fig. 11i) and the divisions of the brain into prosencephalon, mesencephalon and metencephalon (Fig. 11j) were present at about 6h after hatching. The gill cleft and branchiostegal rays were soon visible (Fig. 11k) and the eyes became markedly protuberant (Fig. 11l). The ventral edge of the notochord often had a thin line of black pigment (Fig. 11j) and the dorsal edge was generally less pigmented. In some larvae, melanophores appeared along the anterior neural spines and ribs (Fig. 11f) just after hatching. The dorsal edge (Fig. 11f, i and j) and ventral edge (Fig. 11f and i) of the tail musculature had a thin line of pigment. The latter region also had about seven large melanophores situated just above the edge (Fig. 11f and j). These were able to expand and contract to form a continuous (Fig. 16d) or broken (Fig. 16c) line of pigment. At 18h after hatching, the divisions along the centra of the vertebrae (Fig. 16a and b) and the first melanophores on the head region appeared (Fig. 16a). Shortly after this, a large prominent melanophore developed posterior to the caudal peduncle along the ventral edge of the musculature (Fig. 16b and e) and a patch of black pigment appeared antero-ventrally on the abdomen. At 22h small teeth appeared close to the anterior edge of the lower jaw and alignment of the reticulation on the fin fold of the caudal fin, the precursors of the fin rays, were apparent (Fig. 16c). At 1d 7h numerous melanophores appeared along the intestine and the swim bladder was heavily pigmented (Fig. 16d). The pectoral fins, now quite long, were often seen above the body outline (Fig. 16e and f). The remaining oil globule if still present was situated anteriorly in the yolk (Fig. 16f), and at 2d after hatching most larvae (exception Fig. 16g) had utilized at least half of their yolk (Fig. 12). Abrasion of the fin fold was occasionally seen in larvae of this age. At 2d 8h precursors of the bony structures of the skull (Fig. 16i), and the ramifying nature of the large expanding and contracting melanophores lying ventrally along the tail (Fig. 16j) were evident. The liver was now

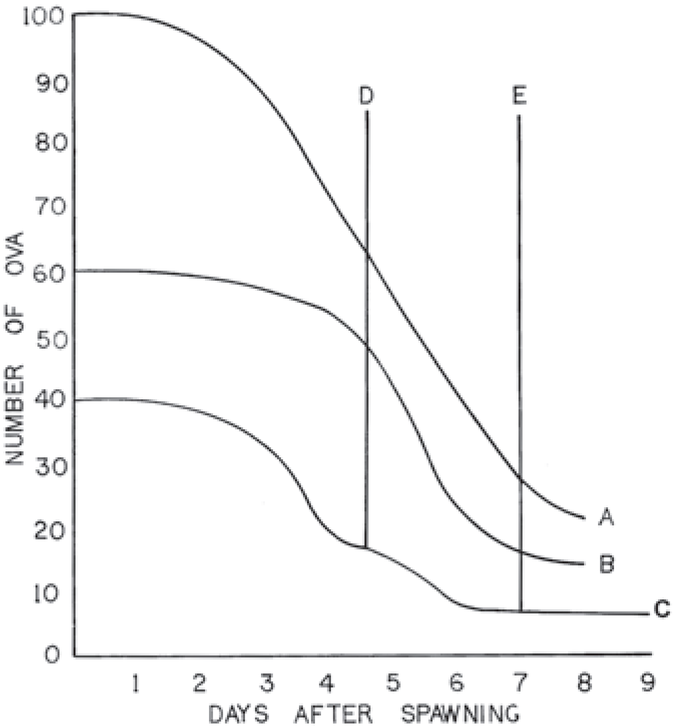

Figure 14. Survival of eggs and larvae from three different batches (A, B and C), when temperatures fluctuated between 17.2 and 22.0^0C, until just after hatching. D - hatching commenced; E - hatching finished. Mean survival at 8 days after spawning 21.5%.

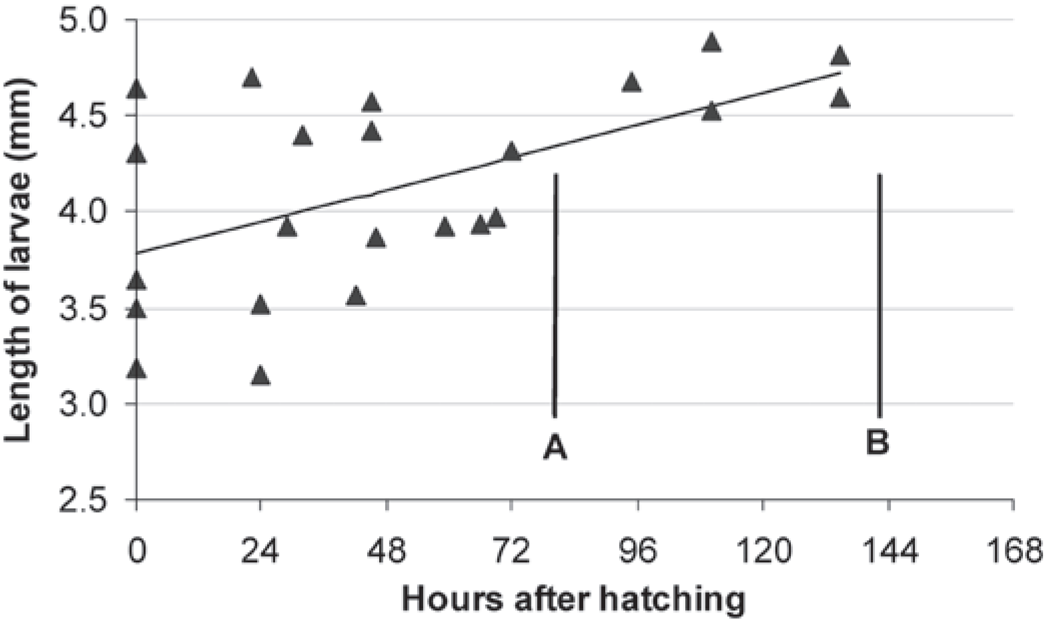

Figure 15. Relationship between length of larvae and hours after hatchings. A, approximate termination of prolarval stage; B, time by which all larvae had died. The line was determined by linear regression, $y=0.007x + 3.778$, ($r^2= 0.326$, $P=0.004$). The spread of larval length at hatching results from lack of agitation of eggs and low temperatures which delay hatching.

obvious (Fig. 17a and b) when the remaining oil globule if present was very small. At 2d 18h only a small amount of yolk remained (Fig. 17b and c). The dorsal view of the prolarva (Fig. 17d) showed protuberant eyes, large otic capsules, long pectoral fins, a black swim bladder and mid-dorsal stripe, and the partly pigmented intestinal region. A usual sign of sick larvae at this stage (Fig. 17e) was a curvature of the tail. Peristalsis in the intestine was first observed at 3d, when numerous melanophores were present along the intestine (Fig. 17f), indicating the approach of active feeding and the end of the prolarval stage. However some slow developing or early hatched larvae still had some yolk (Fig. 17g and 18a). For most prolarvae all the yolk had been utilised (Fig. 17h) and the body form was streamlined (Fig. 17i) by 3d 16h, signifying the end of the prolarval stage.

Post larvae

Observations on post larvae were limited and on juvenile fish were nil, because all larvae died shortly after the commencement of the post larval stage, probably due to an inadequate source of larval food.

Post larvae were normally 3.95mm in length when first reaching this stage at about 3½ d after hatching (=10d after fertilization). Other dimensions are provided below[3]. At 3d 20h the enlarged pericardial sinus showing the heart (Fig. 18a) and the gills and branchiostegal rays (Fig. 18b and c) were clearly visible. Protrusion of the anus (Fig. 18c) indicated the existence of peristaltic movements in the intestine and defecation, and the inter-vertebral spaces were apparent. The distribution of melanistic pigment was characteristic for the species at this time, with between seven and nine large contractile melanophores along the ventral edge of the musculature of the tail between the anus and the caudal peduncle. Their contractability and variability is emphasised in Fig. 18d-h. The large ventral melanophore, posterior to the caudal peduncle; and the mid ventral melanistic patch just posterior to the opercular opening were prominent. Food was first observed in the pigmented intestine (Fig. 18d) at about 4½d after hatching, (see liver in Fig.18d, e and f). The fin fold was either diminishing antero-dorsally (Fig. 18g) and in the region of the caudal peduncle, or else it varied in extent in different post larvae. A thin line of pigment also occurred postero-dorsally along the musculature on many post larvae (Fig, 18f). The liver continued to enlarge around 8d when food was clearly visible in the stomach (Fig. 18h), and the gill cover was observed moving and the gill cleft was clearly visible (Fig. 18i). The oldest post larva observed and photographed (4.95mm in length) was 12d 15h after hatching (Fig. 18j). This post larva had an extensive array of pigment and had been progressively darkening in colour. The fin rays had commenced to form in the caudal fin. The fin fold in the region of the caudal peduncle had also nearly gone. Although food was present in the intestine, no post larvae survived beyond this stage.

Adults

From a pond stocking followed by a successful spawning (Fig. 3), it was evident that *P. grandiceps* grew quite rapidly and was able to spawn at one year old. Large females and males often died shortly after spawning. Since females larger than 8cm in length were seldom seen, they probably only survive two years and spawn twice (see Fig. 3). The largest male collected was 11cm in length. Males and

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[3] Dimensions in millimetres of post larvae at 3½d after hatching are:- swim bladder 0.22x0.11; eye diameter 0.25; lens 0.11x0.07; otic capsule 0.18x0.14; and depth of body at abdomen 0.90.

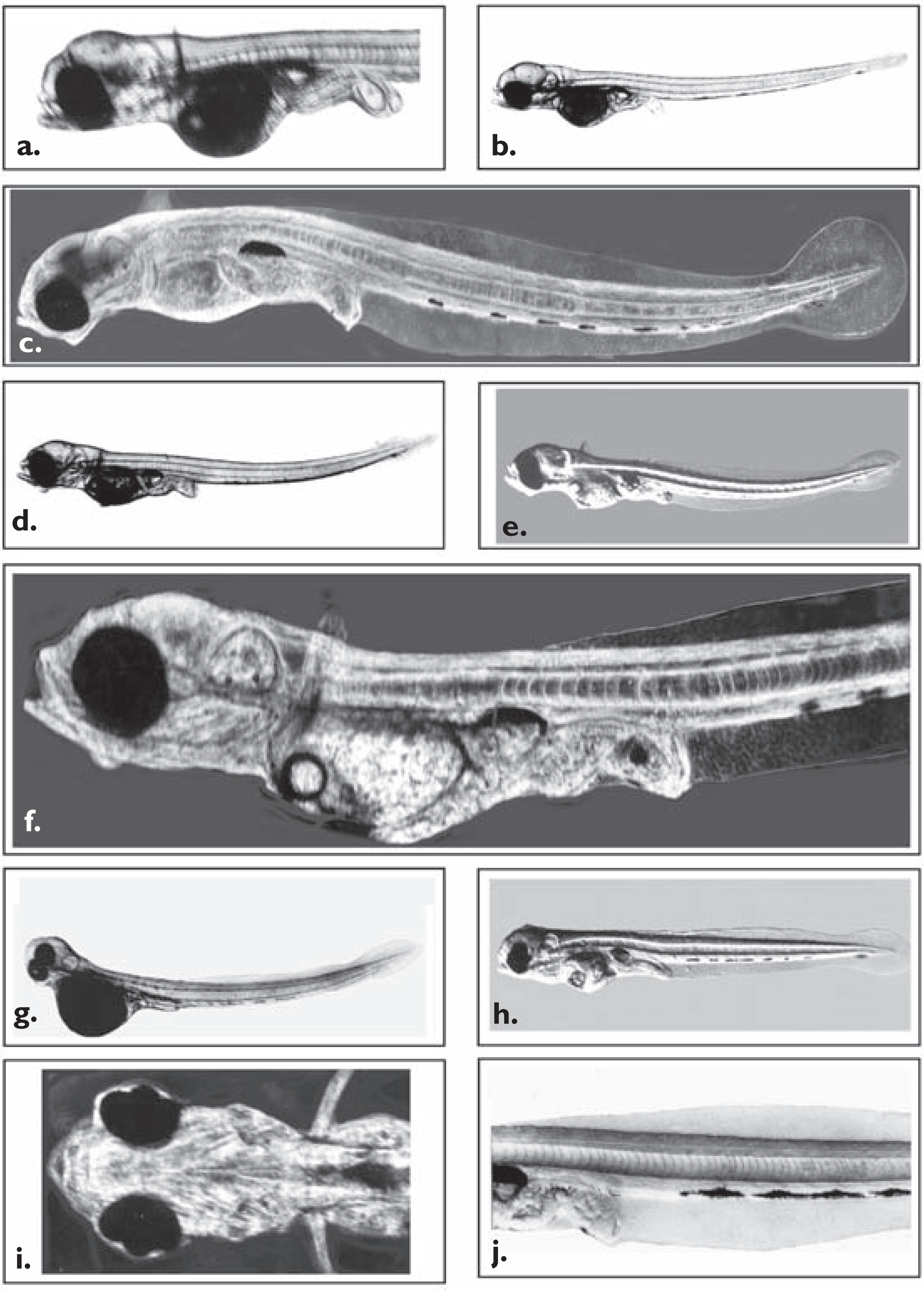

Figure 16. Larvae of P. *grandiceps*, times given are after hatching (d = days, h = hours and m = minutes). (a) 17h 10 m - divisions in centrum of vertebral column, long pectoral fin and melanophores on head region; (b) 23h 24m - well developed mouth; (c) 22h 25m - phase contrast composite photograph showing pigmented dorsal region of swim bladder and reticulate nature of fin fold with alignment of reticulation in the dorsal region; (d) 1d 7h 40m - melanophores occurring along the intestinal region; (e) 1d 8h 5m - dark ground photograph to show the extent of the fin fold; (f) 1d 14h 50m - phase contrast composite photograph showing otoliths in the otic capsule and a single oil globule in the anterior region of the yolk; (g) 1d 18h 22m - a larva which hatched early, still possessing a large amount of yolk; (h) 1d 22h 30m - melanophores on yolk just below oil globule; (i) 2d 8h 50m - phase contrast photograph of dorsal view of head region showing its development and the long pectoral fins; (j) 2d 10h 36m - divisions in centrum and melanophores along ventral edge of body musculature.

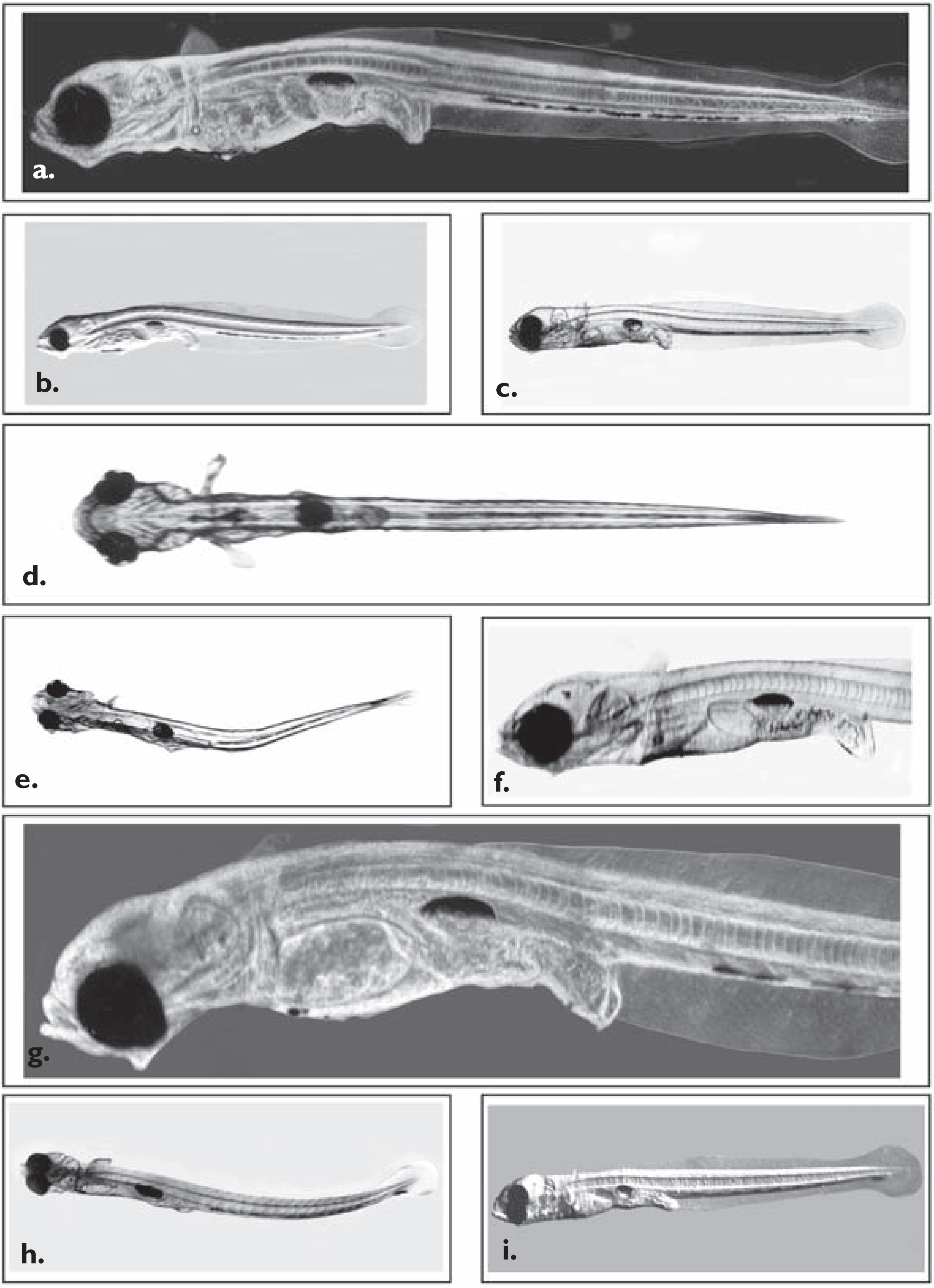

Figure 17. Larvae of *P. grandiceps*, times given are after hatching (d = days, h = hours and m = minutes). (a) 2d 9h 30m - composite phase contrast photograph showing yolk much reduced in size and small oil globule remaining; (b) 2d 10h 47m - distinct melanic patch below yolk; (c) 2d 17h 50m - melanophores spreading ventrally on swim bladder and single large melanophore ventrally near caudal peduncle; (d) 2d 17h 50m - dorsal view showing general structure; (e) 2d 19h 40m - skoliotic condition commonly seen in sick fish; (f) 3d 4m - increasing number of melanophores in region of intestine and liver clearly visible anterior to swim bladder; (g) 3d 1h 15m - composite phase contrast photograph showing more yolk remaining than is normally found in a larva of this age; (h) 3d 7h 2m - yolk mass completely utilised and prominent melanophore near caudal fin; (i) 3d 16h 40m - body well streamlined.

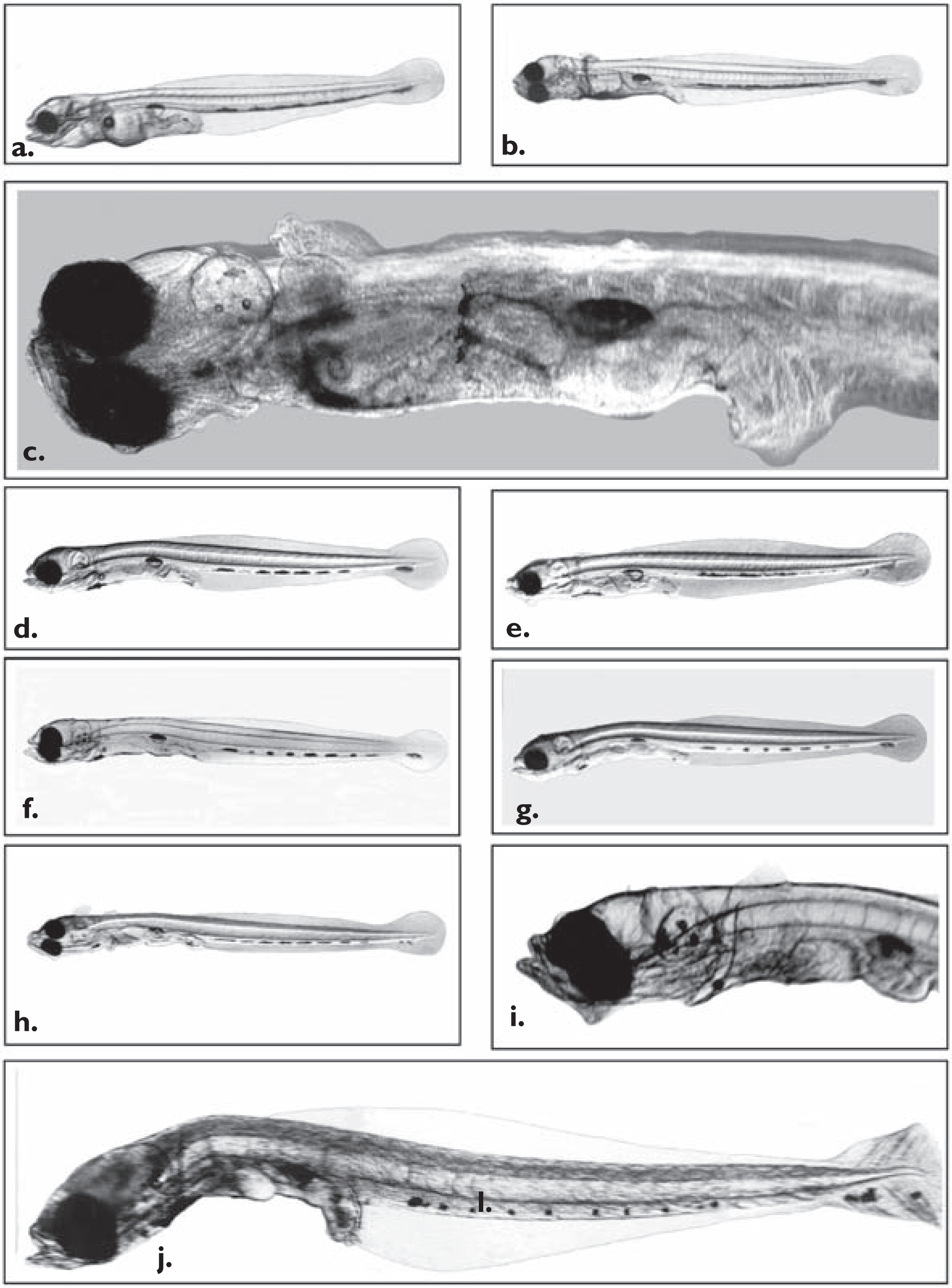

Figure 18. Larvae of *P. grandiceps*, times given are after hatching (d = days, h = hours and m = minutes). (a) 3d 19h 2m - an early hatched larva with still some yolk remaining; (b) 3d 19h 2m - melanophores present laterally along the ventral edge of the tail musculature; (c) 3d 20h 15m - composite phase contrast photograph, dorso-lateral view showing inter-vertebral spaces; (d) 4d 12h 40m - myotomes of tail clearly visible and melanophores present along the intestine with the first sign of food within gut; (e) 4d 15h 42m - yolk mass completely gone and liver clearly visible; (f) 5d 15h 40m - thin line of pigment along dorsal edge of tail region; (g) 5d 18h 40m - dorsal fin fold starting more posteriorly than normal; (h) 7d 22 h - food present in stomach; (i) 9d 15h 25m - gill cleft clearly visible; (j) 12d 15h 40m - composite photograph showing food in intestine, indication of ray development in caudal fin and decrease in fin fold in region of caudal peduncle.

females could only be readily distinguished from external characters during spawning. Compared with a female, the male was generally larger, very dark in colour, and his mouth larger and head broader and more swollen.

The background colour of adults is usually transparent yellowish / green variously blotched; however occasionally it varies from reddish brown, to brown, to black dorsally and laterally. Dorso-lateral blotches (Fig. 1a), particularly near the dorsal fins, were more pronounced in large fish. In some there was a line of irregular blotches mid-laterally, ending in a pronounced dark spot at the base of the caudal fin. This dark spot was present from mid-prolarval stage onwards and appeared to be a reliable characteristic for *P. grandiceps*. Four or five diagonal dark lines occurred on the side of the silvery abdomen. Three stripes radiated from the eye, one from the back of the eye running postero-dorsally over the operculum and another postero-ventrally over the preoperculum. A third thin stripe stretched ventrally from the lower edge of the eye to the angle of the mouth. Their ventral surface was palest, with only the abdominal region being silver to silvery yellow in colour. As breeding approached, both sexes often possessed a row of white to pink square patches, three to four in each row, each side of the mid-ventral line between the base of the pelvic fins and the vent (Fig. 1c and d). Between these rows the skin was fairly transparent, and the internal structure, including the ova of ripe females, could often be seen. The anterior dorsal fin had two pale longitudinal stripes and the posterior dorsal fin three or four pale longitudinal stripes. The anal fin generally had one or two very faint stripes and the caudal fin 7-9 irregular bands formed by dark and pale markings along the fin rays. The other fins and the background colour of those fins described were clear yellowish to greyish yellow in colour. Fin markings were often very faint.

Differences in the urinogenital papillae of the sexes were apparent at breeding when they were much enlarged. The male had three small papillae at the tip (Fig. 1e) and the sides of the urinogenital papilla were concave making the tip moderately pointed. In the female the central small papilla was absent, the sides of the urinogenital papilla were convex to straight and the tip was rounded. There also appeared to be a mid-ventral groove along the female papilla and a swelling anterior to the urinogenital papilla and surrounding the posterior edge of the vent.

Mature males were found as small as 50mm in length and 0.998g in weight but females were much larger being around 68mm in length and 2.234g in weight. Small males were never seen to pair and in all cases they were larger than the females with which they paired.

Gonads

Because of the very low numbers of fish available, the ovaries of only five specimens were examined (Table 3). Spawning observations indicated mean egg size at spawning was around 0.75mm. In females collected from Prospect Reservoir on 9.x.69, the diameter of large ova within the ovary averaged 0.66mm in diameter, indicating that they were close to spawning. The highest G.S.I. recorded was 11.92. Both G.S.I and ova diameter indicated that spawning took place from mid October onwards in coastal areas of New South Wales. In one female which died (G.S.I = 2.80), the largest portion by volume of the ovary was made up of digenean parasites, which grossly inflated the true G.S.I. This fish had been maintained in an aquarium for six months on a diet of earthworms, with the exception of two feeds of tadpoles about 8d previously. It is possible that the tadpoles were the secondary hosts of this parasite. The fecundities recorded (Table 3) were 1557, 833 and 2020 for fish of lengths 68, 75 and 78mm respectively. The 75 mm fish, taken in May 1970, was from an aquarium, which had been heated to induce spawning outside the normal breeding season.

In many fish sampled, testes were transparent and too small to find. Developed testes sampled reached up to one fifth of the total body length. They were paired, the right being slightly longer than the left (Fig. 1f). The highest G.S.I recorded in males was 0.27 (Table 4). The specimens detailed in Table 4 had all been retained in aquaria, some heated, which accounted for high G.S.I's at different times of year. Since some immature fish had a G.S.I. of 0.23, it is predicted most ripe fish would have a GSI greater than 0.23. The testes of one fish were parasitised with digenea.

The spermatozoa of *P. grandiceps* had a head measuring 0.0024x0.0030mm with a tail varying in length from 0.021 to 0.028mm. The anterior region of the head was rounded, but the posterior region was bilobed and the tail was attached to a point between these lobes.

DISCUSSION

The detailed breeding biology of *P. grandiceps* described in this paper greatly expands the published data to date. Pusey *et al.* (2002) had summarised the current knowledge of *P. grandiceps*. Stead (1907) identified *P. grandiceps* as being suitable for keeping in small aquaria and, when discussing the gudgeons, with which he placed this species, he said "the eggs were deposited on objects beneath the surface, and to which they are attached by a sticky secretion from the parent." Breder and Rosen (1966) indicated that in the Eleotridae, the males were

Table 3 Reproductive status of female *P. grandiceps* caught at Prospect Reservoir. nc, ova not countable; hp, ovaries heavily parasitised.

Capture date	Weight of fish (g)	Length of fish (mm)	Ovary weight (g)	Fecundity nos. ova	Gonosomatic index
9.x.69	2.2339	68	0.1611	1557	7.21
9.x.69	3.2310	74	0.0679	nc	2.10
4.v.70	3.5780	75	0.0600	833	1.68
9.x.69	3.5530	78	0.4236	2020	11.92
23.iv.70	5.2582	79	0.1472	hp	2.80

Table 4. Reproductive status of male *P. grandiceps* caught at Prospect Reservoir 1969-1970.

Capture date	Weight of fish (g)	Length of fish (mm)	Testes weight (g)	Gonosomatic index	Comments
9.x.69	0.6837	44	0.0016	0.23	Immature
9.x.69	0.9114	48	—	—	Immature
9.x.69	0.9977	50	0.0022	0.22	—
18.viii.68*	1.2720	53	0.0022	0.17	—
2.x.69	1.8640	60	0.0031	0.17	Testes 4.0 x 1.0mm and parasitised
2.x.69	3.1160	70	0.0037	0.12	—
12.x.69	2.5876	71	0.0033	0.13	Testes length 14mm.
2.x.69	4.8970	84	0.0037	0.08	—
2.x.69	7.1411	92	0.0194	0.27	—
11.x.69	7.9177	93	0.0169	0.21	Bred in aquarium. Testes 17.5x 0.8mm.
—	6.6994	94	0.0051	0.08	testes 4.0 x 1.0mm.
8.x.69	8.0715	95	—	—	Testes not found
21.iv.70	10.6390	105	0.0248	0.23	—
4.v.70	13.3190	110	—	—	Testes not found

*Specimen collected from Wyangala Dam.

often larger than the females and possessed longer fins and brighter colours, and that a pairing display took place. They also stated that eggs were demersal with adhesive threads or a pedestal, and that the male built the nest or selected a nesting site and guarded and usually aerated eggs. The finding in this paper confirms these observations.

In New South Wales fresh waters there are twelve species of eleotrid fishes recognised; of which four still have no scientific name (one *Philypnodon* sp. and three *Hypseleotris* sp.). Most of these species prefer sluggish, weedy waters or lakes and some enter estuaries. The breeding biology of only four of these has been fully described to date, *Hypseleotris compressus* (Auty 1978), *Hypseleotris galii* (Anderson *et al.* 1971), *Hypseleotris klunzingeri* (Lake, 1967) and *Mogurnda adspersa* (Llewellyn, 1971, 2006). In all cases they have an adhesive disc on the egg similar to that in *P. grandiceps*, but the size and shape of the egg differs. In species of *Hypseleotris* so far described, the eggs were smaller, always being less than 1mm along their longest access, and either spherical, oval or pear-shaped. The elongate tear drop shaped eggs of *P. grandiceps* resembled most closely the elongate elliptical eggs of *M. adspersa*. As well as their distinct shape, *P. grandiceps* eggs differed from *M. adspersa* in the non-diffuse nature of their oil globules within the yolk which occurred during most of the larval development.

In addition to size and shape of the egg, the adhesive disc provides another point of difference from other species. *Melanotaenia fluviatilis* (the Rainbowfish, Family Melanotaeniidae) also has a cluster of adhesive fibers, which is typical of the family, but the eggs are spherical, up to 1.15 mm in diameter and are dispersed randomly when spawned (personal observation). The only native freshwater species in inland New South Wales known to have eggs with a totally adhesive chorion, are without adhesive discs or filaments (*Maccullochella peelii peelii*, *M. macquariensis*, *Maquaria australasica*, *Gadopsis marmoratus* and *Retropinna semoni*). All other native species from this area described to date have spherical, pelagic or demersal, essentially non adhesive, eggs.

Differentiation between species of larvae is more difficult. The eyes of only two other described eleotrid larvae were pigmented at hatching (i.e. *H. galli* and *M. adspersa*). The shape of the gut and position of the anus, which was 2/5 of the way along the body in *P. grandiceps*, were useful characters for identification purposes. The distribution of melanin and melanophores in *P. grandiceps* was also different from other described species.

The breeding biology of *P. grandiceps* closely resembles that of *M. adspersa* (Llewellyn 1971, 2006), although breeding displays were not as active or impressive as those observed in *M. adspersa*. In both species, intensive feeding was required for at least three weeks before spawning commenced. Rises in water level were not required as a spawning stimulus and successful spawnings occurred over quite a wide temperature range. The range (18.0 to 28.0oC Table 2) suggests that the spawning season in the wild in the Euston area stretches from mid October to April when river temperatures are in the same range (Llewellyn 1978). This suggestion is consistent with data from Humphries *et al.* (2002) who collected larvae of *P. grandiceps* in the Campaspe River from October to April over 4 years with one occurrence of an August breeding.

Both *P. grandiceps* and *M. adspersa* established a territory with defined spatial requirements, prepared a nest site, and carried out activities such as site cleaning, excavating, spiraling, wriggling, fanning, brood care by the male and guarding or charging. The general spawning behaviour was less elaborate, and spiraling behaviour was far less frequent in *P. grandiceps*, and the yawning behaviour was not seen in *M. adspersa*. Adult *P. grandiceps* were short lived and grew much more quickly (maturing at one year old) than *M. adspersa* (maturing probably at two year old) (Llewellyn 2006).

Lack of breeding success of *P. grandiceps* in at least some aquaria could have been due to the absence of both sexes. However, they did not breed with greater than eight fish present in a 90L aquarium, which suggested that there was a minimal spatial requirement for successful spawning. This may be associated indirectly with competition for food.

In the limited specimens examined, the fecundity of *P. grandiceps* (833-2020)) (Table 3), was slightly higher than in *M. adspersa* (262-1300) (Llewellyn 1971, 2006), but the G.S.I. of males was lower (up to 0.27 and up to 2.15 respectively) (Table 4). This low fecundity of *P. grandiceps*, and hence its relatively low recruitment potential, render it of little value as a forage fish for use as food in the commercial production of larger fish species. Also its low recruitment potential increases its vulnerability in the light of declining water quality and habitat loss. Despite this, populations on the coast seem fairly secure but inland populations are patchy and their status is uncertain.

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